# Hearts, neck posture and metabolic intensity of sauropod dinosaurs

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Hypothesized upright neck postures in sauropod dinosaurs require systemic arterial blood pressures reaching 700 mmHg at the heart. Recent data on ventricular wall stress indicate that their left ventricles would have weighed 15 times those of similarly sized whales. Such dimensionally, energetically and mechanically disadvantageous ventricles were highly unlikely in an endothermic sauropod. Accessory hearts or a siphon mechanism, with sub-atmospheric blood pressures in the head, were also not feasible. If the blood flow requirements of sauropods were typical of ectotherms, the left-ventricular blood volume and mass would have been smaller; nevertheless, the heart would have suffered the serious mechanical disadvantage of thick walls. It is doubtful that any large sauropod could have raised its neck vertically and endured high arterial blood pressure, and it certainly could not if it had high metabolic rates characteristic of endotherms.

**Keywords:** sauropod; dinosaur; heart; blood pressure; neck posture; principle of Laplace

## 1. INTRODUCTION

Since the discovery of sauropod dinosaurs, the function of their long necks has been controversial. The current consensus is that some of these animals were terrestrial browsers, possibly capable of feeding in the canopies of Mesozoic forests (Bakker 1971, 1978; Dodson 1990; Gunga *et al*. 1999; Paul 1998). However, one unsolved problem with a tall, upright neck is the requirement for an exceptionally high arterial blood pressure and an enormous heart (Hohnke 1973; Lillywhite 1991; Poupa & Ostadal 1969; Seymour 1976). Potential solutions to the problem have been proposed, including accessory hearts (Bakker 1978; Choy & Altman 1992) or a siphon mechanism in the neck (Badeer & Hicks 1996; Hicks & Badeer 1992a). This study re-evaluates the problem with new data on scaling of heart-muscle stress, considers the proposed solutions and evaluates a new solution that links heart size with metabolic intensity.

## 2. THE PRINCIPLE OF LAPLACE: BLOOD PRESSURE AND HEART SIZE

Pressure increases with depth in any column of fluid that is supported by a vessel. Judging from estimated vertical distances between the heart and head of erect-necked sauropods, arterial blood pressure at the heart reached over 700 mmHg (93 kPa) (Gunga *et al*. 1999; Hohnke 1973; Millard *et al*. 1992; Seymour 1976). Such pressures would have required a very thick-walled ventricle, because cardiac muscle adaptively adjusts its dimensions to normalize the cross-sectional stress in response to pressure and volume loading, both ontogenetically and phylogenetically (Ford 1976; Mirsky 1974). Wall thickness depends not only on internal blood pressure, but also on the inner radius of the ventricle wall, according to the principle of Laplace. This principle accounts for the difference in right- and left-ventricle

thickness in mammals and birds, and is the major determinant of heart mass in vertebrate animals. A recent analysis of left-ventricular stress in 36 species of living mammals and birds weighing 14 g to 4080 kg shows that stress is similar (mean = 14.5 kPa) in both groups, although birds have arterial blood pressures about 50% higher than mammals (Seymour & Blaylock 2000) (figure 1). Stress in the grossly thick giraffe heart is also normal, despite arterial blood pressures about twice the mammalian norm. Heart mass averages about 0.26% of body mass in 13 species of ectothermic amphibians and reptiles (Poupa & Ostadal 1969), compared to 0.93% in 81 species of endothermic birds and mammals (Poupa & Ostadal 1969), in line with ectothermic systemic blood pressures about a third of endothermic levels (Johansen 1972; Seymour 1987).

In evaluating sauropods, we assume that their hearts were four chambered, as proposed for dinosaurs in general (Seymour 1976) and recently confirmed in an ornithischian fossil (Fisher *et al*. 2000), pumped blood with the same oxygen-carrying capacity as do birds and mammals, and operated with an end-diastolic ventricular stress value of 14.5 kPa (Seymour & Blaylock 2000). We use the exact spherical model of the thick-walled ventricle, in which stress ($\sigma$; kPa) is related to internal pressure ($P$; kPa) and inner ($r_i$; cm) and outer ($r_o$; cm) radii of the walls (Mirsky 1974) by the equation

$$\sigma = (Pr_i(4r_i^2 + r_o^2 + r_ir_o))/(4(r_o^3 - r_i^3)). \qquad (1)$$

Ventricular masses are calculated from the radii assuming a complete spherical shell with a muscle density of $1.06 \mathrm{\,g\,cm}^{-3}$. Allometric equations for estimating cardiac variables are derived from 36 species of mammals and birds (Seymour & Blaylock 2000), but they are similar to equations in earlier studies (Bishop 1997; Günther 1975; Holt *et al*. 1968; Stahl 1967). In these animals, the left ventricle averages 70% of the heart mass. To be conservative, we assume that stroke volume ($V_s$) and end-diastolic volume ($V_{ed}$) scale directly with body mass ($M_b$), although

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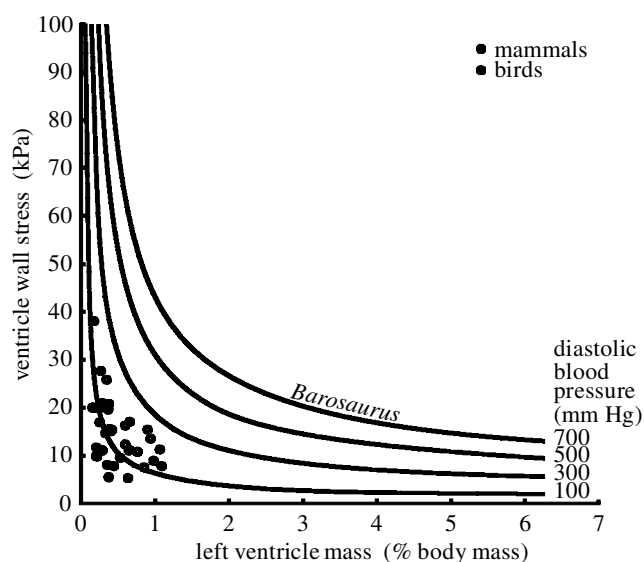
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Figure 1. Theoretical curves relating left-ventricular wall stress, relative left-ventricular mass and internal blood pressure in endothermic vertebrates, according to the principle of Laplace. Points are empirical data from living mammals (filled circles) and birds (open circles) with blood pressures between 80 and 210 mmHg (Seymour & Blaylock 2000).

exponents in other allometric studies are slightly higher than 1.0 (Bishop 1997; Günther 1975; Holt *et al.* 1968; Stahl 1967). End-diastolic volume ($V_{ed}$) in mammals is 1.5 times $V_s$ (Calder 1981). To avoid the equations being overly influenced by small mammals, we fit the equations to include data from a 4080 kg African elephant. The calculated $V_{ed}$ is 7.82 l in the measured 22.6 kg elephant heart (Seymour & Blaylock 2000). With these values, the allometric equations become $V_{ed} = 0.00191 M_b^{1.0}$ and $V_s = 0.00128 M_b^{1.0}$. As a confirmation, $V_{ed}$ in the elephant heart is 8.42 l according to other allometric predictions (Holt *et al.* 1968). Heart rate ($F_h$) scales according to $F_h = 227 M_b^{-0.23}$ in mammals (Seymour & Blaylock 2000), so cardiac output ($CO = F_h V_s$, 1 min$^{-1}$) is assumed to scale according to $CO = 0.29 M_b^{0.77}$.

## 3. HEART MASS OF *BAROSAURUS*

To begin, it is instructive to compare an endothermic *Barosaurus* weighing 40 tonnes (Dodson 1990) to a fin whale of the same size. The whale's heart weighs about 190 kg, or 0.5% of the body mass (Lockyer 1981). The left ventricle weighs about 135 kg and has a wall 10.4 cm thick when relaxed. Its end-diastolic blood volume would be about 76 l and it would pump 51 l with every beat. With a heart rate of about 20 beats min$^{-1}$, which accords with actual measurement (Lockyer 1981), its cardiac output would be about 1000 l min$^{-1}$. Such a heart would operate with a normal wall stress if the systemic arterial blood pressure were 100 mmHg (13.3 kPa), which is a reasonable value for mammals in general (Seymour & Blaylock 2000).

For an endothermic *Barosaurus* to produce 700 mmHg arterial blood pressure, with a ventricular wall stress of 14.5 kPa, the left ventricle alone would weigh about two tonnes, or 5% of body mass (figure 2). In diastole, it would be 52 cm thick and measure about 1.6 m across but

the internal chamber would be the size of the whale's, only 52 cm wide (upper diagram, figure 2). In short, the ventricle would be 15 times heavier than the whale's ventricle, five times thicker but pump the same amount of blood per beat. About 10% of the resting metabolic rate of humans is due to energy use by the left ventricle (Van Citters *et al.* 1957). Both cardiac work rate and metabolic rate scale with body mass to about the same power in mammals (Holt *et al.* 1968), so it is reasonable that this fraction holds for a 40 000 kg whale with normal blood pressure. Therefore, the 15-fold larger ventricle of an endothermic *Barosaurus* would account for about 62% of the animal's resting metabolic rate (which would consequently be 2.4 times that of the whale).

Not only would the enlarged heart be energetically costly, it would also be grossly inefficient because a greater proportion of energy would be used to deform the heart muscle itself and less could be used to propel the blood (Rushmer 1970; Weber *et al.* 1986). In the human heart, about 10% of the total energy is used to overcome ventricular wall stiffness, compared to up to 25% to move the blood (Van Citters *et al.* 1957). Wall stiffness results from tension between muscle layers and from deformation of structural components such as collagen, the amount of which increases with hypertrophy (Weber *et al.* 1986). This effect has been demonstrated as an increase in tension-related energy use in mildly hypertrophic hearts of laboratory animals (Hamrell & Alpert 1986). If energy loss in the walls is directly proportional to wall thickness, then the cost of deforming the ventricle wall of *Barosaurus* could become twice that required to pump the blood.

## 4. PROPOSED SOLUTIONS

To solve the problem of enormous cardiac hypertrophy in sauropods, auxiliary hearts in the neck have been proposed (Bakker 1978; Choy & Altman 1992), but this idea is unlikely, not only on physiological and anatomical grounds (Millard *et al.* 1992), but also on evolutionary grounds. For an auxiliary heart to be effective, it would require both a pulsatile wall and valves. Selection for pulsatile arterial walls would not occur unless valves were present, and selection for valves would not occur unless pressure gradients in the neck caused reverse flow. Reverse arterial flow does not normally occur in vertebrates, and none has arterial valves.

The principle of the siphon has also been discussed in relation to the necks of sauropods (Badeer & Hicks 1996; Hicks & Badeer 1992a). Negative (sub-atmospheric) cranial blood pressures down to −570 mmHg (−76 kPa) have been postulated for *Barosaurus* (Badeer & Hicks 1996). The idea is that gravity affects the arterial and venous blood columns equally, and the descending venous blood facilitates the rise of arterial blood. Hence, the heart does not work against gravity and a thick heart is unnecessary. This siphon concept is controversial (Hicks & Badeer 1992b; Seymour *et al.* 1993), but it is not important to restate the debate here. It is necessary only to demonstrate that severely negative blood pressures in the head were not possible.

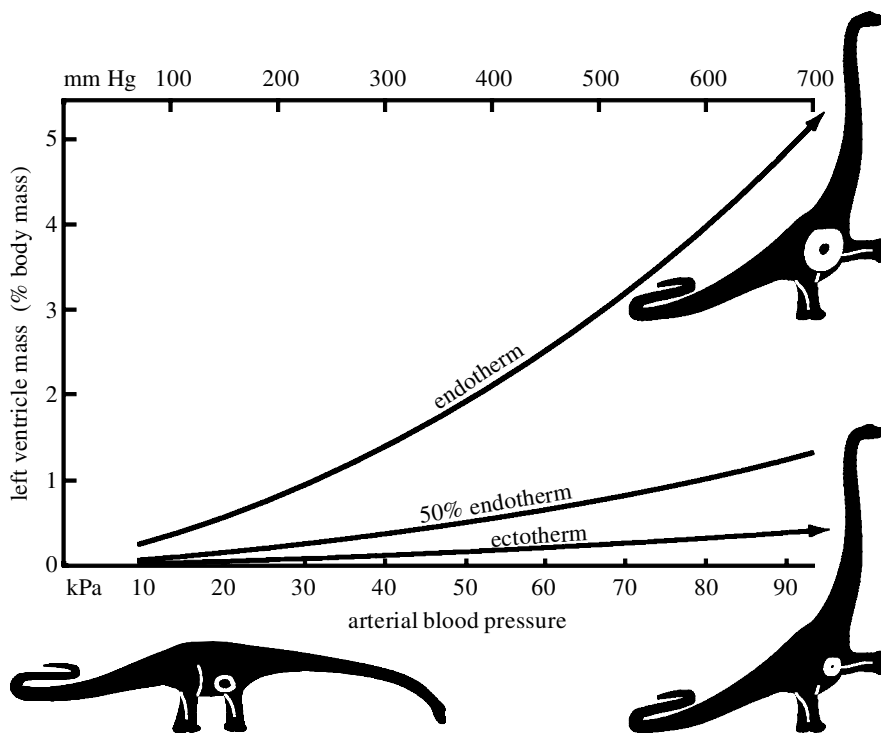If the vessels are capable of collapse, then a negative pressure would cause them to close completely and stop

Figure 2. Relationships between systemic arterial blood pressure and the mass of the left ventricle according to the principle of Laplace and assumed blood-flow rates characteristic of endothermic mammals, ectothermic reptiles and an intermediate level. Scaled diagrams of left-ventricular wall thickness are superimposed on *Barosaurus* silhouettes, according to models for low-pressure endotherms (bottom left), high-pressure endotherms (top right) or high-pressure ectotherms (bottom right).

blood flow. However, negative pressure in the circulatory system can occur if the vessels are prevented from collapse, either by attachment to rigid structures or envelopment by tissue that is also under negative pressure. The classic example is the negative venous pressure measured inside the skull of upright humans (Rushmer 1970). Gravity creates negative pressure at the top of the cerebral–spinal fluid column, and the pressure is transferred through soft tissue to intracranial blood vessels. For negative arterial pressures to occur in the head of a *Barosaurus*, however, all of the vessels in the head and neck would require protection, including the major arteries and veins in the neck, as well as the microcirculation inside and outside the cranium. The neck vessels could be protected by the scaffolding of the derrick-like cervical vertebrae and overlapping cervical ribs, prominent in sauropods, and they might have had a venous drainage through the bony vertebral plexus that could not collapse (Batson 1944). The skin also might have possessed bony dermal plates (Dodson *et al*. 1998) or other dense tissue that might have prevented collapse of all blood vessels.

Despite theoretical mechanisms for creating negative pressures in the head, there are at least two vital reasons why this would be impossible. First, negative pressures in the body fluids of animals are dangerous because of the potential for gas-bubble formation in the blood. Although blood pressure in *Barosaurus* could not decrease to −690 mmHg (−92 kPa) and cause the blood to boil (Badeer & Hicks 1996), dissolved gases can come out of solution at less extreme pressures. Formation of nitrogen bubbles in the blood during a drop in environmental pressure can block small vessels and cause decompression sickness, or 'the bends'. Sauropods' blood equilibrated with air in the lungs at atmospheric pressure. As it passed up the neck and experienced negative pressure, the dissolved

nitrogen would have become supersaturated and might have formed bubbles. Aviators can get the bends at 3300 m altitude where barometric pressure is 510 mmHg (68 kPa) (Hills 1977), which is equivalent to a drop of blood pressure to −250 mmHg (−33 kPa). Goats form gas bubbles when flown above 4300 m (Hill *et al*. 1994), equivalent to a drop in blood pressure to −320 mmHg (−43 kPa). These results involved relatively slow aircraft ascents during which some desaturation of the blood occurred, whereas the trip to the *Barosaurus* head would occur quickly and no desaturation would be possible. No definite level of pressure reduction can be set for bubble formation, because the appearance of bubbles is variable between subjects and the physiology of nucleation is not fully understood. However, if blood pressure dropped to −570 mmHg in a fully erect sauropod, bubble formation is likely.

Another problem of negative pressures in the circulatory system is the danger of aspiration of air into a damaged vessel. If all vessels in the head were protected from collapse, then they could not close if damaged. Negative pressure would draw the blood away from the wound, which, without a clotting system, could not seal and heal in the usual way. Surface tension in the cut vessel might prevent the blood from being withdrawn but we calculate that if the blood pressure were only −100 mmHg (−13 kPa), air would be sucked into an open vessel of 22 μm diameter, about the size of a human arteriole. Without clotting or collapse, there would be nothing to stop air from entering all of the superior vascular beds from an invisibly small wound.

There are further problems with negative pressures in the vascular system of the head that could be insurmountable. It is difficult to imagine protecting all vessels in the head from collapse, in particular the flexible ones associated with the jaw and sensory organs. A positive

pressure would be needed to keep these beds open. Negative blood pressure would prevent filtration of fluid from the blood into the interstitial fluid and eliminate lymph flow completely. The consequences of this for tissue fluid balance, removal of proteins from tissues and transport of lymphocytes are potentially dire.

An alternative proposal that would reduce or eliminate negative pressures in the head is to stiffen and squeeze the lower parts of the circulatory system, such that most of the arteries and veins are under inherently high pressure, without the added pressure of the heart (Badeer & Hicks 1996). At chest level, therefore, both arterial and venous pressures would be extraordinarily high, decreasing predictably to a point high in the neck where pressures would approach atmospheric level. This is the so-called hydrostatic indifferent point (HIP) of the circulatory system, where ideally there are no passive changes in blood pressure resulting from changes in posture (Gauer & Thron 1965). However, moving the HIP upward would increase the systemic venous pressure at the heart, and this pressure would be transferred through the right ventricle to the lungs, potentially causing filtration of fluid into the airspace (oedema) or even rupture of pulmonary capillaries. Pulmonary arterial blood pressures in endothermic vertebrates remain in the region of 10–15 mmHg (1.3–2.0 kPa) to prevent this (Smits 1989). It is entirely possible that a high resistance in the pulmonary arteries could reduce blood pressure in the capillaries, but this would mean that the blood leaving the lung would also be at low pressure and therefore could not stretch the left myocardium during filling to store much energy. Therefore, the left ventricle would have to produce a systolic pressure more than equivalent to the height of the systemic arterial blood column above the heart, regardless of the location of the HIP. Exceptionally high systemic blood pressures would still be required. The only way to reduce the size of the heart would be for it to move up the neck with the HIP (Seymour *et al.* 1993). However, the lungs would also have to move up the neck, because if they did not, the pulmonary venous column would create a back pressure and result in pulmonary oedema or capillary rupture. Short of proposing that both the heart and lungs were in the necks of sauropods, we conclude that such a position of the HIP would not assist circulation to the head. The exact position of the sauropod heart is not known, but a recent fossil ornithischian dinosaur reveals the heart in the expected place beneath the ribs (Fisher *et al.* 2000).

## 5. HEART SIZE AND METABOLIC INTENSITY

A new solution to the erect sauropod's cardiac problem is to propose that end-diastolic volumes, and hence stroke volumes, were smaller than previously assumed. Smaller stroke volumes would require smaller hearts that would have to either beat faster or reduce the rate of blood flow. If sauropods had ectothermic metabolic rates, then their blood-flow requirement would be about 10–20% of the endothermic level (Bennett & Dawson 1976). If cardiac output of a 40 000 kg sauropod were 140 l min$^{-1}$ (20% of the whale), then an 11.5 kg ventricle (as occurs in a 3200 kg elephant) would easily produce 100 mmHg blood pressure, pumping at 35 beats min$^{-1}$ and a stroke volume

of 4 l. To produce 700 mmHg, however, the ventricle would thicken to 165 kg, or 0.4% of the body mass (figure 2). Even if the cardiac output were reduced to 50% of the endothermic level, assuming intermediate sauropod metabolic rates (Farlow 1990; Spotila *et al.* 1991), 700 mmHg could be produced with a 530 kg ventricle that is nearly the same proportion of body mass (1.3%), as in giraffes. However, it is important to realize that, despite the reduction in size and energy demands, the ventricle would have the same relative thickness in comparison to end-diastolic volume (the thickness approximately equal to the diameter of the internal blood space), and would suffer the same mechanical inefficiency resulting from high wall stiffness. In addition, a heart rate of 35 beats min$^{-1}$ seems very high for a 40 000 kg animal, be it an ectotherm or an endotherm. It has been elegantly demonstrated that heart rate scales inversely with body size, because it is determined by the characteristics (resistance, compliance and length) of the arterial tree and the requirement for myocardial perfusion (Westerhof & Elzinga 1991). Expected heart rates would be lower than 20 beats min$^{-1}$, which would require proportionately larger end-diastolic volumes and thicker ventricles. Ectothermy may solve the problem of heart size, but it leaves some serious problems of cardiac mechanics.

## 6. CONCLUSION

We conclude that large sauropods were unlikely to have carried their necks erect, but it may have been possible if they had metabolic rates considerably lower than expected for endotherms. The metabolic status of sauropods is debatable (McIntosh *et al.* 1997; Paladino *et al.* 1997; Paul 1998) but ectothermy is suggested by the uninsulated skin of well-developed sauropod embryos (Chiappe *et al.* 1998). Whatever the metabolic reality, it appears that high metabolic rate and upright neck posture were mutually exclusive in sauropods. If some genera such as *Diplodocus* and *Apatosaurus* were incapable of lifting the head high, because of movement limitation of the cervical vertebrae (Stevens & Parrish 1999), they avoided high blood pressure and could have had high or low metabolic rates; but if the anatomy of genera such as *Brachiosaurus* required them to hold the head 7.9 m above the heart (Gunga *et al.* 1999), the animals were unlikely to have been endothermic.

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